

VARIATION IN THE SILVERING OF *ARGYNNIS*
(*SPEYERIA*) *CALLIPPE* IN THE INTERIOR
MOUNTAIN AREA OF
SOUTH CENTRAL CALIFORNIA

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IN A COMPREHENSIVE STUDY of the geographic variation of *Argynnis (Speyeria) callippe* Boisduval, based on examination of about 2750 specimens from many localities well distributed throughout the range of the species in California, Hovanitz (1943) recognized several main divisions of this species complex. Among them are the "South Coast Range Population" extending from the San Francisco Bay area southward through the Coast Ranges into Lower California and the "Western Sierra Nevada Populations" extending in a band along the western Sierra Nevada, at moderate elevations from the region west of Lassen Peak southward to about the Greenhorn Mountains at the southern end of the Sierra Nevada. He found that these two population groups are connected through a "Southern Zone of Intergradation" by a "series of steps across the Piute Mountains, the Tehachapi Mountains and the Sierra Madre Range."¹

He characterizes the populations in the Southern Zone of Intergradation as follows:

"From the Santa Monica Mountains on the coast, where the typical *callippe* of this (the South Coast Range) region lives, it is found that in going inland (Charlton Flat, Mint Canyon and 'Ridge Route') the lightness of all colors increases. The butterfly becomes smaller and the light colored band and spots on the upper surface of the wings tend to become obliterated, leaving a more uniformly colored wing surface such as is present in the western Sierra Nevada gradient. However, the yellow-brown color is very much lighter than in the latter and the band on the under side of the hind wings is still yellow; the spots are still always fully silvered. The tendency toward these conditions is the more marked the farther from the coast and the farther into the Tehachapi Range the populations exist. In the Tehachapi Range, the butterflies are very lightly colored and the band on the upper surface of the wings is rare; the spots are still silvered. At Havilah, Piute Mountains, the population consists of some silvered, some unsilvered and some intermediate spotted

¹This range is not named on many maps. It lies parallel to, and south of, the middle portion of the Cuyama River which is the long north branch of the shorter Santa Maria River shown discharging into the ocean at about lat 35° in Fig. 1.

individuals (this is the type locality of *macaria* Edws.); the exact frequency of these types is not known, but there is a high percentage of silvered and unsilvered present . . . In the Greenhorn Mountains, the segregation into a silvered population on the eastern side of the summit and an unsilvered one on the western side is decidedly apparent, though mixing occurs toward the south, where the populations unite".

The main purpose of this paper is to describe semi-quantitatively the variation of silvering within the Southern Zone of Intergradation. The silvery decoration of animals is far less common than the pigmental coloration. While Hovanitz (1941) has found general qualitative correlations of the pigmental coloration of butterflies with environmental conditions, he finds the significance of silvering in *callippe* "quite incomprehensible" (Hovanitz, 1943, p. 420). Some peculiarities of the silvering data revealed by the semi-quantitative treatment in this paper suggests that studies of its physico-chemical nature and genetic control might be rewarding. An hypothesis is advanced as a point of departure for such studies.

THE SAMPLES

The material for this study consists of complete series of *callippe* that I collected during June 8 to 15, 1957 in company with Fred T. Thorne, and one sample from Bouquet Canyon consisting of part of a series taken in 1952 by Thorne and kindly given to me. In breaking the series Thorne exercised no conscious selection for color or pattern, though worn and damaged specimens were discarded.

Parallel or convergent evolution among the Argynnids in some regions presents problems of species identification. In the Southern Zone of Intergradation this problem arises between *callippe* and *coronis* Behr. The latter, as the subspecies *hennei* Gunder, flies with *callippe* and resembles it so closely that confident identification requires either great familiarity with both species or known series from the region for comparison. L. P. Grey is in possession of both and kindly reviewed my field identifications. These had been made in consultation with Thorne. At the time neither of us had previous acquaintance with *hennei*, though we were both familiar with several other subspecies of *coronis*. Two specimens I had labelled *callippe* proved to be undoubted *coronis*. One labelled *callippe* came back from Grey with the notation, "Could this be *coronis*? (Don't ask me!." Another labelled *coronis* bore Grey's notation "I think it is a *callippe*." The last two, when spread and compared with the now-available good series of *hennei*, appear to me to be undoubted *coronis*, though the under side wing surface (the only surface exposed to Grey's examination) is remarkably like the *callippe* from the same locality. These four specimens have been excluded from the samples.

In the list that follows, the collections are grouped by localities. Each group contains mainly specimens taken at one location, to which have been added a few specimens from nearby locations. Those

in the main group, I believe, are members of a single interbreeding colony; the others may consist of strays from the same colony in some instances, and in others, may be strays from some other colony. All localities are in Kern County except Sandberg's and Bouquet Canyon which are in Los Angeles County. Distances from named places are given to the nearest mile (1.61 km) measured on a straight line on large-scale road maps. Directions, also determined from such maps, are referenced to true North and stated in Mariners' abbreviations appropriate to the 32-point compass. Thus southwest is given as SW, southwest by west as SWxW and west southwest as WSW. These are 11.25° steps and allowing for measuring inaccuracy are correct to about the nearest 15°. Elevations were taken by aneroid altimeter graduated in 100-foot (30.5 m) units and probably accurate to ± 200 feet. Botanical names are according to Jepson (1923 - 1925), Abrams (1940, 1944 and 1951) and Abrams and Ferris (1960). Nomenclature of the butterflies follows the list by McDunnough (1938) except for the genus (*Speyeria*), which, at the species and subspecies level follows the arrangement of Dos Passos and Grey (1947).

A. EAST SLOPE, GREENHORN MOUNTAINS. June 12, 1957, 18 males and 1 female taken 6 miles WSW of Kernville, elevation 4900 ft., along the road leading steeply from Isabella Reservoir to Greenhorn Mountain Park passing between Tittle and Rattlesnake Creeks, in association of Digger Pine (*Pinus sabiniana* Dougl.), Oak (*Quercus* sp.), California Fremontia (*Fremontia californica* Torr.), and chaparral broken by grassy areas, with Yerba Santa (*Eriodictyon* sp.) flowers as nectar attractant; included in addition is 1 male taken 8 miles WxS of Kernville, elevation 5500 ft., Transition Zone, in a small roadside opening in Yellow Pine (*Pinus ponderosa* Dougl.) and Incense Cedar (*Libocedrus decurrens* Torr.) forest.

B. WEST SLOPE, GREENHORN MOUNTAINS. June 12, 1957, 58 males and 6 females taken 27 miles NE of Bakersfield, elevation 3300 ft., near the foot of Eugene Grade, in Digger Pine, Blue Oak (*Quercus douglasii* Hook & Arn.) and grass association, with violets (*Viola* sp.) abundant; included in addition are 3 males and 1 female taken 26 miles NNE of Bakersfield, elevation 3000 ft., in Blue Oak and grass association, with riparian flora along a small creek.

C. HAVILAH. June 11, 1957, 13 males and 1 female taken 2 miles S of Havilah, elevation 3100 ft., Digger Pine, mixed oak and chaparral association with riparian flora along a small creek, mostly attracted to Yerba Santa flowers; in addition are 1 male from 1 mile north of Havilah, elevation 2800 ft., and another from 5 miles S of Havilah, elevation 3900 ft.

D. WALKER BASIN. June 11, 1957, 30 males and 6 females taken 10 miles SxW of Havilah, at the south end of Walker Basin, elevation 3200 ft., Blue Oak and Grass association with sagebrush and violets. Hoarhound (*Marrubium vulgare* L.) attracted a few individuals, but most were taken in the characteristic slow, fluttering flight displayed when on breeding grounds.

E. TEHACHAPI. June 14, 1957, 12 males and 7 females taken 8 miles W of Tehachapi (the town), elevation 4700 ft., at the eastern end of Bear Valley in Blue Oak and grass association, with patches of sagebrush (*Artemisia tridentata* Nutt.), mostly attracted to Wallflower (*Erysimum* sp.) flowers; in addition are 3 males from 7 miles W of Tehachapi, elevation 4600 ft., and 1 female from 3 miles SW of Tehachapi, elevation 4600 ft.

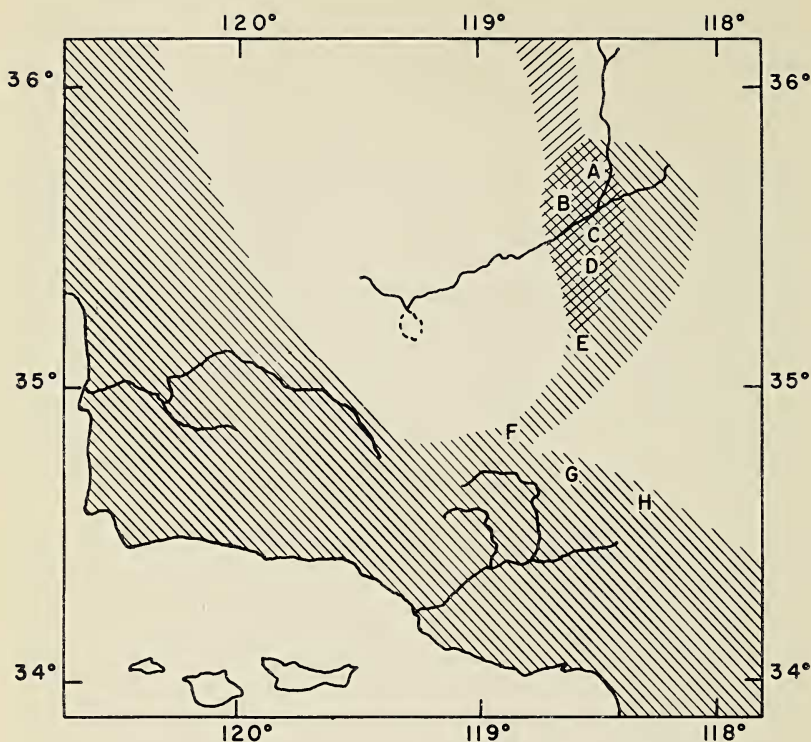


FIGURE 1. Location of populations sampled (letters "A to H") superimposed on the distribution of *Argynnis (Speyeria) callippe* (shaded area) adapted from a portion of Hovanitz' map (1943, Fig. 1) showing the distribution of the "silvered spots" character by shading lines slanted upward to the left and the "unsilvered spots" character by shading lines slanted upward to the right. The Kern River (upper right) separates the Greenhorn Mountains to the north from the Piute Mountains to the south as it flows to a sink in the lower San Joaquin Valley (blank area at upper middle). At middle left is the Santa Maria River with the Cuyama River as its long north fork. At the lower right is the Santa Clara River. The crests of the higher mountains and ridges of the transverse series of ranges lie north of the Santa Clara River Drainage and south of the Cuyama River.

F. LEBEC. June 8, 1957, 24 males and 8 females; June 9, 1957, 26 males and 4 females; and June 15, 1957, 11 males and 15 females; total, 61 males and 27 females taken 1 mile S of Lebec, elevation 3600 ft., in oak and grass association with adjacent chaparral including sagebrush (*A. tridentata*), Buckwheat Brush (*Eriogonum fasciculatum* Benth.) and Yerba Santa; some were at flowers of the last, others in breeding-ground flight.

G. SANDBERG'S (on old Ridge Route). June 9, 1957, 12 males and 3 females; June 15, 1957, 1 male and 2 females; total, 13 males and 5 females taken 9 miles ESE of Gorman in Digger Pine and sagebrush (not *A. tridentata*) association, with violets. Breeding ground behavior was predominant.

H. BOUQUET CANYON. June 11 and 12, 1951, 18 males collected by Fred T. Thorne at "upper Bouquet Canyon, 4 miles down from Pine Creek — Lake Hughes road" (estimated 16 miles W of Palmdale, estimated elevation 3400 ft.).

HABITAT AND MESOSCALE DISTRIBUTION

According to these records *callippe* in this region occupies elevations from 2800 to 5500 feet, but occurs in good concentrations only between 3100 and 4900 feet, generally, the upper portion of the Upper Sonoran Life Zone. Its habitat is marked characteristically by scattered Blue Oak, Digger Pine, and sparse chaparral with sagebrush (*A. tridentata*) often present. Usually there are broad areas or small patches of grass present. Practically all of the localities are in grazing land, but at the time of our trip it was being very lightly grazed.

Violets were noted at only three of the locations. Where they were seen, the plants were abundant, mature, with fully-developed seed capsules and appeared about to dry up. Where violets were not seen, either they had dried up already, or the collecting was of members of the colony that had been drawn by nectar sources somewhat away from the site of the larval food plant.

During the trip we collected at 31 locations within the geographic range and elevation limits of this butterfly. Of these, seven obviously were in, or close to, *callippe* colonies; five locations yielding only one or several specimens, evidently were not as close; and the remaining 19 locations where we took none probably were distant from colonies, though this may not have been true for a few places where we sighted an Argynnid or two which could have been either this species or *coronis*. These indications favor a population model consisting of well-separated, compact colonies from which individuals do not stray often or far. This pattern is more accentuated in this region than in most others within my collecting experience.

Butterflies of 30 other species were taken at one or another of the seven locations where *callippe* were caught in good numbers. *Plebeius acmon* West. and Hew. and *Hesperia lindseyi* Holland were the most ubiquitous, occurring at most locations from the Greenhorn Mountains to Sandberg's. The former were taken in small numbers while the latter, in some locations were very abundant. In addition to these, the most common and prevalent in the Greenhorns and the Piutes were *Euphydryas chalcedona* Doubleday and Hewitt, *Melitaea palla* Boisduval, and *Strymon saepium* Boisduval; while through the Tehachapi to Sandberg's they were *Minois silvestris* Edwards and *Argynnis coronis* Behr. If one of the specimens whose identification was questioned by

Grey is, as I believe, *coronis*, this species extended north at least to Havilah. Inasmuch as all *coronis* taken on this trip were fresh males, and in other regions within my collecting experience *coronis* flies somewhat later than *callippe*, it is likely that a week or two later in the season *coronis* would have been found to be even more consistently a companion of *callippe*.

RELATIVE ABUNDANCE

The relative abundance in butterfly populations may be significant in studies of variation. From records extending through many years, Ford (1945) found that a rapid increase in abundance of the colonial butterfly *Euphydryas aurina* Rott was accompanied by "an extraordinary outburst of variation". When the increase ceased, the colony settled down to a comparatively uniform type, different from the one prevailing prior to the increase. Scientists differ as to the interpretation and significance of this phenomenon as a mechanism in evolution. Whatever the interpretation, if the generality of this phenomenon is to be ascertained, records must be accumulated through the years for a number of butterfly populations.

To this end, there are placed on record in Table 1, estimates of relative abundance of *callippe* in each of the seven colonies sampled in 1957. This estimate is in terms of catching rate and assumes that the number caught in unit time is proportional to the abundance of the population in the area of collecting. It is homologous in concept to the measure "catch per unit of effort" almost universally and successfully (sometimes "calibrated" to a absolute abundance by tag-and-recapture experiments) used as a basic statistic in studying the dynamics of fish population fluctuations (Ricker 1940). For *callippe* I have computed the catching rate, R, according to the formula:

$$R = \frac{N_c}{H - k N_t}$$

where N_c is the number of *callippe* caught, H is the time, in hours, in the collecting period, N_t is the total number of specimens of all species caught (including *callippe*) during the collecting period, and k is a constant whose value depends on the methods and dexterity of the collector in caring for a specimen once it is in the net. By timing myself in the caring, individually, for each of 150 specimens of a number of species from all families except Megathymidae under typical field conditions, I found my k value to be 0.0155 hours (37.8 seconds).

In repeated samplings of several species I have found R to be surprisingly stable. For *callippe*, the three samplings at Lebec are an example of this. Although stable, R as computed by this formula should

be regarded only as a first-order approximation, or index, of true relative abundance, because it is affected by systematic error and several sources of variability, not all of them random. A more sophisticated iterative treatment theoretically should improve R, but it involves assumptions of uncertain merit awaiting test.

TABLE 1. Relative abundance in terms of catching rate, R, in number per males and by the per cent of the males that were fresh.

Locality, date (1957) and elevation	Catching rate (R)	Per cent of males	Per cent fresh
A. E. slope, Greenhorns, el. 4900 ft., June 12	* 39	84	86
B. W. slope, Greenhorns, el. 330 ft., June 12	** 227	91	52
C. Havilah, el. 3100ft., June 11	16	93	15
D. Walker Basin, el. 3200 ft., June 11	* 44	83	87
E. Tehachapi, el. 4600 - 4700 ft., June 14	33	67	79
F. Lebec, el. 3600 ft., June 8	24	75	84
F. Lebec, el. 3600 ft., June 9	24	87	69
F. Lebec, el. 3600 ft., June 15	30	42	45
G. Sandberg's, el. 4000 ft., June 9	17	80	75

In the meantime, of most concern is that R increasingly underestimates abundance as the latter increases, presenting simultaneous catching opportunities more often and usually avail can be taken of only one of them at a time. Recognizing this, the values in Table 1 that probably were moderately underestimated owing to this factor are marked with an asterisk, and the one value that was grossly underestimated is marked with a double asterisk. At the other end of the scale, when only one or two specimens are caught during a collecting period, R has large error owing to random variability of incidences of encounters. Avoiding this, Table 1 gives catching rates computed for only the first-listed location under each locality, except for Tehachapi where the times and catches of the first two locations were pooled for computing the catching rate.

Another error source is that as kN_t approaches H, a small error in k produces a large error in R. This approach was not close enough to be critical for the values given in Table 1, though the value for the west slope of the Greenhorn Mountains may have been moderately affected.

Every collector can think of a number of other obvious sources of error or variability such as weather conditions, unusual concentrations at attractants, etc., These obvious ones can be avoided by comparing only sets of samplings taken under reasonably similar conditions, as is true for the set in Table 1 except as later noted.

Of course the catching rate reflects the relative abundance only at the stage of flight at which the collecting was done, and may yield values departing substantially from the inherent abundance. An esti-

mate of the stage of the flight is afforded by the relative numbers of fresh and worn individuals. In Table 1, recorded as "fresh" were individuals without readily perceptible random loss of scales or fringe. Damage reasonably attributable to accidental causes, such as notches, tears, breaks and rubbed streaks or patches was not considered. The data are given for males only, there not being enough females to yield reliable percentages. The two sexes were not combined for this statistic because this would introduce extraneous variability owing to the tendency of females to emerge later than males. As evidence of this, only four of the 53 females listed in Table 2 were worn. More direct evidence is afforded by the Lebec samples. Those of June 8 and 9 were mostly males and mostly fresh. About a week later more than half of the males were worn and the females, all fresh, outnumbered the males. The sample from Havilah is anomalous in respect of percentage worn in relation to sex ratio. Although most of the males were worn, only one female was taken. Probably the greater ease of collecting males at the Yerba Santa flowers diverted us from the females which probably were widely scattered for ovipositing in the adjacent area which appeared to be the likely habitat for violets, though the plants were not observed, doubtless having dried up before our visit. At Sandberg's the catching rate was substantially depressed by a strong breeze sweeping the exposed slope and wafting many a disturbed butterfly out of stalking or pursuit range.

Appraising the catching rates in the light of these qualifying factors, the presence of some worn males at all localities indicates that the *callippe* flight was well developed throughout the region. But the high percentage of fresh males and the scarcity of females suggests that the flight had not yet reached its peak at most localities except Lebec where it probably was near peak stage on June 15 and Havilah, where the male flight had apparently passed its peak. Allowing for the differences in stage of flight and the collecting difficulties at Sandberg's, it appears that relative abundance was capable of attaining a height-of-flight index of 30 to 40, probably closer to the latter, at all localities except the location on the west slope of the Greenhorn Mountains where abundance was at least an order of magnitude higher, and at Walker Basin where it probably was substantially higher than 40 per hour, though well below that on the west slope of the Greenhorn Mountains. Although we did not trace out the geographic extent of a colony in any of the localities, the impression gained while collecting, was that these two colonies covered more extensive areas than the rest. It may be concluded, first, that the samples were drawn from near the middle of the flight period and hence probably represent nearly the modal characteristics of the population in each colony; and second, the colonies varied quite widely in population size, perhaps through more than one order of magnitude. Further results may emerge if comparisons with changed levels of abundance become possible in the future.

VARIATION IN SILVER SCALING

The silver scaling in *callippe*, as in Argynnidids generally, is confined to certain pattern elements on the ventral wing surface. For the most part these are well defined spots in the apical and subapical area of the fore wing and all well defined spots in all areas of the hind wing. In addition, on heavily silvered individuals, silver scales may form ill defined streaks along the inner margin and in some of the interspaces between spots in the basal and discal areas of the hind wing. The present study is confined to the well defined spots of the hind wing. When unsilvered these spots are a light buff color, usually sharply bordered or outlined by brown scales. Some or all of the spots may be partly silvered. Then the silver scales and buff scales stand out in sharp contrast to each other when specimens are held in the best relation to the light source and the eye to bring out the specular quality of the silver scales.

A fully quantitative measure of the degree of silvering would be the ratio of silvered scales to all scales in the area potentially subject to silvering. To avoid spending a prohibitive amount of time counting scales, I have employed a subjective system of scoring based on general appearance. It would have been desirable, too, to utilize exclusively the pristine fresh individuals, but to avoid reducing the number below levels needed for tests of significance, I have scored the slightly and moderately worn individuals along with the fresh ones, excluding only those whose loss of scales caused serious doubt as to their correct score. The penultimate column of Table 2 shows the number excluded for this reason.

Because the amount of silvering sometimes differed appreciably in the basal and discal area, which will be called "disc" for brevity, from that in the submarginal area, called "margin", the two portions of the wing were scored separately. Four grades of silvering were recognized: Grade 0 for complete lack of silver scales; Grade 1, when there were only flecks of silver well separated by buff scales; Grade 2, when some of the spots were unsilvered, others were partly silvered and still others were fully silvered, or any combination of two of these conditions; and Grade 3, when all spots were so fully silvered that there were no readily perceptible buff scales. The Disc Grade and the Margin Grade were treated as half scores and added together to arrive at the individual Score. Thus there are seven possible scores: 0 to 6, inclusive.

Of the 238 individuals scored, 50 had half scores that differed from each other by one grade point. None differed by more than one. Of the 50 with different half scores, the Disc Grade was higher than the Margin Grade for 40 individuals and lower for 10. Curiously, for the two Greenhorn Mountain samples and the Havilah sample, pooled, the ratio was 33:4, while for the Walker Basin, Tehachapi and Lebec samples, also pooled, it was 7:6. The difference between the ratios 33:4

and 7:6 is statistically significant ($p=0.02$) despite the small numbers in the latter. It is possible that the tendency for the marginal row of spots to be less silvered than the disc spots is linked to the general lack of silvering in the three northernmost localities.

TABLE 2. Frequency distribution of silvering scores

Sex and sample	Score							Mean	Not Scored	Total
	0	1	2	3	4	5	6			
Males:										
A. E. slope, Greenhorns	5	3	1	1	—	2	7	3.16	—	19
B. W. slope, Greenhorns	17	8	7	6	4	8	7	2.42	7	64
C. Havilah	2	1	—	2	—	2	4	3.73	4	15
D. Walker Basin	1	2	1	—	1	2	19	5.08	4	30
E. Tehachapi	1	—	—	1	—	—	13	5.40	—	15
F. Lebec	1	1	1	1	1	1	39	5.54	15	60
G. Sandberg's	—	—	—	—	—	—	10	6.00	3	13
Total	27	15	10	11	6	15	99	4.16	33	216
Females:										
A. E. slope, Greenhorns	—	—	1	—	—	—	—	2.00	—	1
B. W. slope, Greenhorns	—	—	2	3	—	—	—	2.60	—	5
C. Havilah	—	—	—	—	—	—	—	—	1	1
D. Walker Basin	—	—	—	1	1	1	3	5.00	—	6
E. Tehachapi	—	—	1	1	—	—	6	5.01	—	8
F. Lebec	1	—	—	—	—	—	25	5.77	1	27
G. Sandberg's	—	—	—	—	—	—	5	6.00	—	5
Total	1	—	4	5	1	1	39	5.12	2	53

The mean score for males is 4.16 and for females is 5.12 (Table 2), suggesting that females tend toward more silvering than males. But four-fifths of the females were taken at Walker Basin, Tehachapi and Lebec where silvering in both sexes is nearly complete. If we pool these three samples and class together the individuals with scores 0 to 4 inclusive, and similarly those with scores 5 and 6, in order to have high enough numbers for statistical test, we find no significant difference between the sexes ($P = 0.9$). Accordingly, further analysis deals with both sexes combined, as shown graphically in Fig. 2.

The arrangement of samples in Fig. 2 is in ascending order of their means. This also arranges them from north to south except for the reversal of samples A and B. Where samples are near the same parallel of Latitude and have appreciable meridional displacement, as among A, B and C as one group and F, G, and H as another, their means also ascend from west to east.

The slopes of the lines connecting the means in Fig. 2 should not be taken as representing gradients of silvering in the sense of reflecting unit increase of silvering per unit distance. The panels are not spaced in proportion to distance, but merely to accommodate the height of the bars. The means, themselves, are defective because the scores do not represent even gradations in amount of silvering. Further, because of

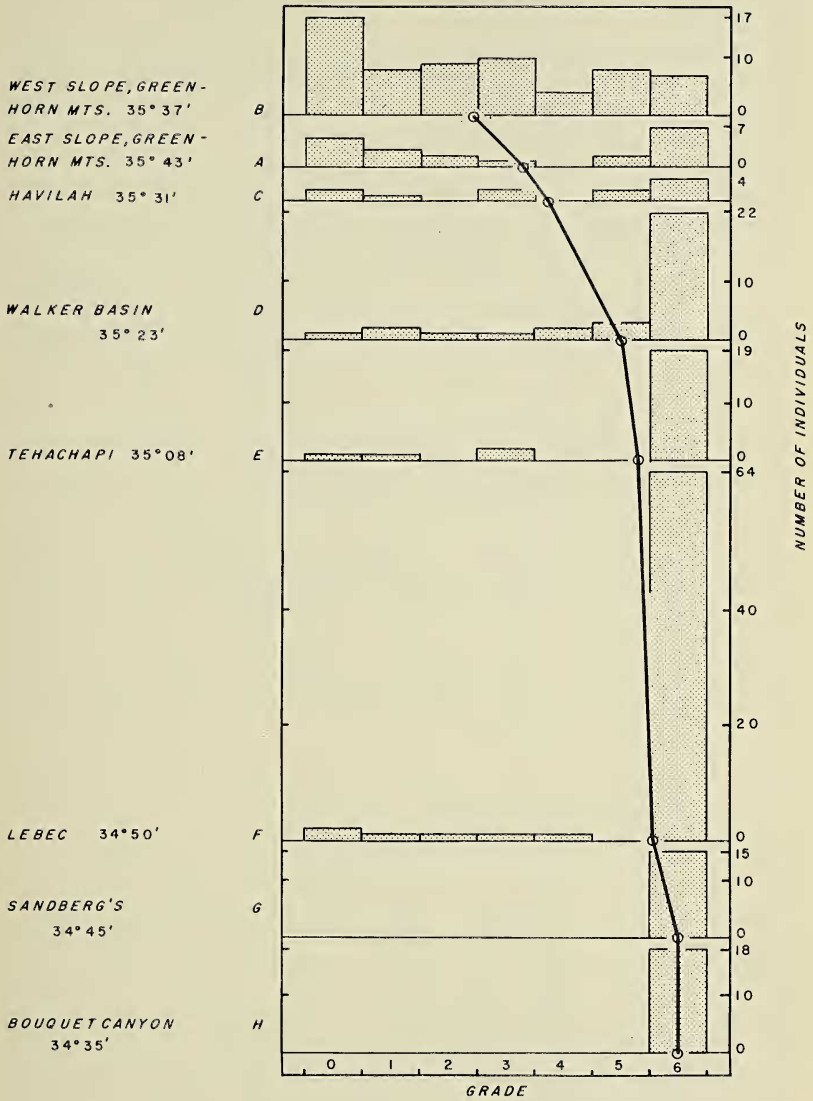


FIGURE 2. The degree of silvering of the several samples, shown as histograms of the number of individuals according to grade (see text); and the mean grades, shown as small circles connected with heavy straight lines.

the prevalence of low numbers at the middle scores, the distributions depart widely from the bell-shaped normal probability curve and the parametric test commonly applied to means would not yield reliable probabilities even if the means were not otherwise defective. The means were computed and connecting lines were supplied in the graph only to give a general perspective of the amount and direction of differences between localities.

For a more careful assessment, the significance of the differences between samples, as to the numbers of individuals falling into the several silvering classes, can be made by the chi-square test which requires neither a normal distribution nor uniform class size. It does require a pooling of the original score classes to provide a minimum of five as the expected number on a class. To meet this requirement, the data have been grouped into two classes: (1) individuals with Scores 0 - 4, which can be described as "unsilvered" and partly silvered"; and (2) those with Scores 5 and 6, which can be described as "silvered or nearly so". With this grouping the approximate probability, *P*, of the difference between any two samples in respect of the ratio of "unsilvered and partly silvered" to "silvered or nearly so" occurring by chance can be found by entering the table of chi-square distribution on one degree of freedom with the value of chi square computed from the 2 x 2 contingency table according to the method given by Fisher (1948, p. 85). For greater precision the Yates correction for continuity was incorporated and *P* was found by graphical interpolation between tabular values. The results are given in Table 3 as a matrix in which the chi-square values between all combinations of pairs of samples are shown in the upper right portion and the corresponding values of *P* in the lower left portion.

TABLE 3. Chi-square values (upper right) and probability values (lower left) between pairs of samples.

Locality and sample	Sample						
	B	A	C	D	E	F	G
W. Greenhorns .. B		2.37	2.97	>10	>10	>10	>10
E. Greenhorns .. A	0.16		0.02	4.63	5.10	>10	7.14
Havilah .. C	0.08	0.50		1.24	1.74	0.83	5.78
Walker Basin .. D	<.001	.03	.19		.05	.84	2.32
Tehachapi .. E	<.001	.02	.18	.50		.64	1.36
Lebec .. F	<.001	<.001	.34	.34	.40		.37
Sandberg's .. G	<.001	.008	.02	.14	.19	.50	

The three northern samples, A, B, and C form a group within which there is no statistically significant difference at the five per cent probability level ($P = 0.05$), and the four southern samples, D to G, inclusive, form another such group. But these groups are not discrete from each other. Sample C from Havilah differs no more significantly from D, E, and F than from A and B, indeed, somewhat less. The sum of chi squares among A, B and C is 5.36; *df* are 3; and *P* is 0.14. The

comparable values among C, D, E, and F are: Chi-square, 5.34; df, 6; P, 0.48. The indeterminate position of Havilah relative to the two groups, most probably is due to the small number in the sample from there. With such a small sample it would require a very strong contrast in silvering ratio to prove statistical significance. Until more material is available it remains uncertain whether the population at Havilah resembles more closely those to the North or those to the South in respect of silvering, or whether it is truly intermediate as suggested by Fig. 2.

Likewise, the sample from the east slope of the Greenhorn Mountains is small and does not test significantly different from that of the west slope. But for the Greenhorn Mountains there are two sources of additional data. Thorne and I scored both his catch and mine while in the Greenhorns and this record includes about twice as many individuals as given in Table 2. We used three categories: "unsilvered", "part silvered", and "silvered", corresponding somewhat inexactly to the Scores 0 - 1, 2 - 4 and 5 - 6, respectively, of Table 2. Hovanitz (1934) reported the number of individuals in a sample from the east side of the Greenhorn Mountains, elevation 5500 feet, and from the west side at Cedar Creek, elevation 5000 feet, according to three categories: "not silvered or very slightly so", "intermediate" and "well - or fairly-well silvered". Assuming these categories correspond approximately to those of Thorne-Sette, the data may be pooled as follows:

East side:

	Unsilvered	Intermediate	Silvered	Total
Thorne - Sette	6	15	17	38
Hovanitz	0	2	14	16
Total	6	17	31	54

West side:

Thorne - Sette	72	24	32	128
Hovanitz	10	8	4	22
Total	82	32	36	150

With more data it is possible to use a 2 x 3 contingency table for a more discriminating test. This yields a probability far less than one in a thousand that the west side and east side samples could have been drawn from a population containing the same proportions of unsilvered, partly, silvered, and silvered members. This does not prove that there is no mixing between the populations of the west and east slopes; it only indicates the extreme unlikelihood of enough interchange to form a thorough mixture. But when it is considered, in addition, that the ridge of the mountain is clothed with transition forest within which no colonies of *callippe* were found, it seems clear that the interchange, if any, must be slight and probably by way of mixing with the more silvered populations to the South at different rates on the two sides of the mountain range as suggested by Hovanitz (1943, p. 411).

Turning southward, past Havilah, there is at Walker Basin a small proportion of unsilvered and partly silvered individuals in the population. The low proportion continues with only slight further diminution in going from Walker Basin in the Piute Mountains, through the Tehachapi Mountains to Lebec. This uniformity suggests a relatively brisk interchange between colonies in this stretch of mountains, probably coupled with strong environmental selection against unsilvered individuals.

Then at Sandberg's, only a short distance beyond Lebec, all individuals are silvered. This is true also for the specimens from Bouquet Canyon (not included in the scoring table because they were only a part of a series). But my sample from Sandberg's is too small to assuredly include unsilvered or partly silvered individuals if they constitute only a small percentage of the population. There is historical evidence, in Gunder's (1930) list of butterflies of Los Angeles County, of the occurrence of unsilvered *callippe* at several localities in the transverse ranges south and southeast of Lebec. Under "*Araynnis macaria laurina* Wri. THE UNSILVERED MACARIA FRITILLARY, a transition form." Gunder recorded one male collected by Comstock "June 10, 1922, Ridge Route;" one male collected by Friday "June 19, 1929, Pine Canyon;" and two males and one female collected by Gunder "June 25, 1921, Bouquet Canyon." "Ridge Route" probably is identical to, or at least near, the locality I give as "Sandberg's"; "Bouquet Canyon" may be identical to, or near the locality of the Thorne collection here listed under the same place name; Pine Valley lies about halfway between the two. The last is definitely on the desert side of the transverse ranges, while the other two localities are near the crest dividing the drainage to the desert from the drainage to the Pacific. The Thorne collection is definitely from the Pacific drainage side. It is probably that this crest marks the southern limit of the unsilvered or partly silvered form.

Reviewing, there is a mixture of unsilvered, partly silvered and fully silvered *callippe* extending through the Southern Zone of Intergradation, from the Greenhorn Mountains in the North, southward through the Piute and Tehachapi ranges, to the crest of the series of ranges extending transversely across California at about latitude 34° 40' N. Most of the change from the predominantly unsilvered condition in the north to the predominantly silvered condition in the South, take place in about the northernmost one-fourth of the Zone. Through the remaining three-fourths, beginning at about the mid-length of the Piute Mountains, where a high degree of silvering already has been reached, the increase in silvering is very gradual. Although it is still perceptibly incomplete at Lebec near the Southern end of the Tehachapi, unsilvered and partly silvered become so rare beyond there that one should not expect to encounter evidence of the unsilvered condition without drawing large samples from the popu-

lation. It is reasonable to conclude that this is the southern limit of the tendency toward lack of silvering in the ventral hind-wing spots of *callippe*. To express this finding in Fig. 1, the area shaded with lines slanted upward to the right should be extended to include localities E, F, G and doubtfully H. When so extended, the southern limit of lack of silvering would more nearly agree with the southern limits of "uniformly colored red-brown upper surface" and "lack of brown pigment between spots on the underside of the hind wings" as mapped by Hovanitz (1943, Figs. 2 and 4).

DISCUSSION

Although this description adds some details to the distributional pattern of silvering in *callippe*, it raises more questions than it answers. Some are concerned with geographic limits. How much farther north does silvering extend? Does it taper off gradually from the western Greenhorn Mountains northward as does the opposite condition from Walker Basin southward, or does it end abruptly a short distance north of the sampled Greenhorn Mountain localities? Does the more silvered population of the eastern slope of the Greenhorn Mountains end as in a cul-de-sac co-terminal with the limits of the Kern River drainage, or does it extend northward as a tongue along the higher Sierra Nevada toward silvered populations such as those near Downieville and Gold Lake?

More perplexing questions concern the processes governing silvering. The distribution of individuals among the seven score classes reveal a paucity of intermediates in the middle of the range (histograms A and C in Fig. 2). Could such a frequency distribution arise from simple Mendelian inheritance, or is a more complex mechanism required?

The existence of intermediate degrees of silvering suggests similarity with the example of simple Mendelian inheritance described by Ford (1945, p. 173) for the Currant Moth, *Abraxas grossulariata* L., which, in its commonest form, has wings with a white background. In its less common form, *lutea* Cockerell, the white is replaced by a deep yellow. When these two forms are interbred the heterozygotes have a pale yellow background. Mating an individual homozygous for white with one homozygous for deep yellow, produces offspring intermediate between the two parents. There is no dominance. Taking this as a model for silvering in *callippe*, and using Ford's system for notation we may use the symbols $C^W C^W$, $C^W C^S$ and $C^S C^S$ for representing the unsilvered (Score 0), the partly silvered (Scores 1 - 5), and the completely silvered (Score 6) phenotypes, respectively. For such a model, in a population containing equal numbers of the two homozygotes ($C^W C^W$ and $C^S C^S$), we should find $C^W C^W : C^W C^S : C^S C^S : 1 : 2 : 1$. None of our samples have equal numbers of homozygotes, but if we pool samples A, B and the ratio is 24 : 51 : 18. This

differs from the ratio 1 : 2 : 1 by no more than one would expect from random sampling variability in about half of the samples drawn ($P = 0.44$). We may conclude that there is no evidence *against* the hypothesis that silvering is controlled by a single pair of alleles the phenotypes scored 1 to 5 may be lumped as the heterozygous component of the population.

However, in the Currant Moth, equal doses for white and for deep yellow produced a color about half way between the two homozygotes. In *callippe* there are very few individuals about half silvered. Individuals scored 3 and 4 comprise less than one-third of the category with scores 1 to 5. Perhaps some more complex genetic system may account for this peculiar distribution within the partly silvered segment of the population. But I am attracted by the idea that some chemico-physical process, such as crystallization may be involved. These tend to be triggered by very slight differences in conditions, and once triggered, go to completion.

In this connection it is also interesting that in areas of potential silvering, the single scales, as viewed with a hand lense, appear either totally buff or totally silver, never in between.

In pursuing this idea, I have found only a little information on the silvery decorations of the Lepidoptera in the literature that bear on its chemical nature. Mayer (1897) makes direct reference to its nature in the Argynnids, saying ". . . Dimmock ('83) has shown that the silvery white and milk-white colorations are due to optical effects produced by reflected light. In the silvery white scales, however, such as the under surface of the hind wings of Argynnis, there must be a reflecting surface toward the observer, for both silvery and milk-white colors appear simple milk-white by reflected light." According to Fox (1953, p. 289) uric acid, derived from chrysalid metabolism, deposited in the wings of the adult butterfly; guanine and uric acid contribute opaque whiteness and glistening silvery aspects. Ford (1945), although discussing extensively the physical and chemical nature of butterfly coloration, is silent on the nature of silvering. Taylor, (1925) points out that guanine (also spelled guanin) deposited in crystalline form imparts the silvery appearance prevalently displayed by pelagic fishes, while bottom fishes with prevalently white under-surfaces have their "subdermal tissues heavily charged with *amorphous* guanin, which is chalky white." He describes guanine crystals, after they have been processed into pearl essence for making artificial pearls, as ". . . very thin light blades, floating in a liquid . . . [which] show their maximum luster when they are oriented parallel to each other . . . [when] pointing promiscuously in all directions, the effect will be a metallic or dull pearly luster."

While one would prefer evidence derived directly by analysis of the substance as it occurs in *callippe*, it is not far fetched to suppose that this substance is guanine, sometimes deposited as crystals disposed

with appropriate orientation to give the specular effect that we call silvery, and sometimes in amorphous form adding whiteness to the pigmental brown to produce the light buff of the unsilvered spots. On this supposition it is necessary that the "silvering gene" control only the conditions within the pupal scale-sac fluid so as to precipitate guanine amorphously for buff scales, or alternatively, as crystals for the silver scales. Presumably, in homozygotes the balance of influences is well to one side of the critical point so that the deposit in all scales is always amorphous, or always crystalline. In the heterozygotes, too, it may take place on the "all or none" basis, but by single scales. Under the equal and opposite influence of the two alleles the equilibrium may be very unstable and readily tipped to one side or the other of the critical point. This could be mediated by very slight differences in environmental conditions of the particular microclimate of a pupal individual at the precise time of color deposition in the scale sacs. This would tend to affect nearly all of the scales of an individual alike, swinging most of them toward one side of the critical point more often than nearly equal numbers to each side. Small differences between members of the colony as to pupation site, date and time of day of deposition of salts in the wing sacs, or even the rate of drying after eclosion, might provide the variety of conditions necessary to produce the observed peculiar frequency distribution of the supposed heterozygous phenotypes.

This set of ideas is not advanced as an explanation, but as an hypothesis inviting test by those having interest and competence in the fields of experimental breeding or biochemistry, or both.

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